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RESEARCH ARTICLE

# Local and landscape characteristics shape amphibian communities across production landscapes in the Western Ghats

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## Abstract

1. Global tropical forests have been modified and fragmented by commodity agroforests, leading to significant alterations in ecological communities. Nevertheless, these production landscapes offer secondary habitats that support and sustain local biodiversity. In this study, we assess community level and species-specific responses of amphibians to land management in areca, coffee and rubber, three of the largest commodity agroforests in the Western Ghats.
2. A total of 106 agroforests across a 30,000-km$^2$ landscape were surveyed for amphibians using a combination of visual and auditory encounter surveys. We used a Bayesian multi-species occupancy modelling framework to examine patterns of species richness, beta diversity, dominance structure and individual species occupancies. The influence of biogeographic variables such as elevation and latitude as well as microhabitat availability of streams, ponds and unpaved plantation roads was tested on amphibian species occupancy.
3. Coffee agroforests had the highest species richness and lowest dominance when compared to areca and rubber. Beta diversity was highest in areca for within agroforest measures. Compared across agroforests, coffee had highest beta diversity with areca and rubber. Both elevation and latitude showed an overall positive association with amphibian occupancy, although species-specific responses varied considerably.
4. Microhabitat availability was one of the strongest predictors of amphibian occupancy, with mean community response being positive with presence of water bodies and roads. Pond presence increased species richness per site by 34.7% (species-specific responses in occupancy ranged from −2.7% to 327%). Stream presence alone did not change species richness but species-specific response ranged from −59% to 273%. Presence of plantation roads also increased species richness by 21.5% (species-specific response ranged from −82% to 656%). Being unpaved with

little vehicular traffic, plantation roads seem to provide additional habitats for amphibians. Presence of all three microhabitats at a site increased species richness by 75%.

5. Our study highlights the importance of land management strategies that maintain diverse native canopy and freshwater bodies and other microhabitats in sustaining amphibian fauna. Market-driven land-use change from coffee to other agroforest types will have detrimental effects on amphibian communities and their long-term sustainability in the Western Ghats.

**KEYWORDS**

agroforests, amphibians, biodiversity indices, community model, microhabitats, occupancy, species richness

## 1 | INTRODUCTION

Amphibians are among the most highly threatened vertebrate taxa, and over one third of all known species are thought to face risk of extinction and another one third are categorized as data deficient (IUCN, 2020; Stuart et al., 2004). There are two global patterns that explain the rate of species declines. First, threats to amphibians have a high degree of overlap with regions of greatest amphibian diversity and endemism (Gallant et al., 2007; Hof et al., 2011). Second, amphibian distributions are under-represented within global protected area networks (Rodrigues et al., 2004). While disease, climate change, invasive species and environmental pollution all pose serious threats to amphibians, the greatest threat remains habitat loss (Hof et al., 2011). Successful conservation thus depends on management strategies that sustain breeding habitats outside protected area, particularly across different human-modified landscapes.

Agriculture is among the leading causes of global land-use change and habitat loss (Phalan et al., 2011). The intensification of agriculture and continuing habitat loss are expected to rise as human populations face increasing concerns about food security (Tscharntke et al., 2012). Studies show that developing tropical countries face highest risk of biodiversity loss, with agricultural intensification having particularly detrimental effects on biodiversity hotspots in Sub-Saharan Africa, India and China (Zabel et al., 2019). These agriculture-induced landscape changes have already modified both structure and function of amphibian communities (Cole et al., 2014; Gallant et al., 2007). Consequently, production landscapes such as commercial forestry and agriculture need to serve an increasing role in tropical biodiversity conservation (Daily et al., 2003; Karanth et al., 2016; Robbins et al., 2015).

In the global tropics, production landscapes such as agroforests do not support the same level of amphibian diversity as primary forests (Faria et al., 2007; Faruk et al., 2013; Gardner et al., 2007; Ribeiro et al., 2018). Agroforests often have communities with lower beta diversity, altered species compositions and increased dominance structure when compared to primary forests (Mendenhall et al., 2014; Murrieta-Galindo et al., 2013; Pineda & Halffter, 2004). Regular disturbance can also lower abundance, survival and population growth rates in individual species (Cole et al., 2014). Nevertheless, many studies show that agroforests provide secondary habitats for much of the native amphibian diversity (Brüning et al., 2018; Guerra & Araoz, 2015). While agroforests are unlikely to replace primary forests, there are opportunities for management of these habitats to improve their biodiversity potential and ecosystem function (Teuscher et al., 2016; Wanger et al., 2009). Determining biodiversity-friendly land management characteristics has received less attention compared to studies that contrast a single production type with native habitats.

Amphibian community assembly at the local scale is strongly influenced by microhabitat availability (De Oliveira & Eterovick, 2010). Heterogeneous vegetation structure, canopy cover, leaf litter and water bodies provide thermal buffering and breeding habitats (Ferreira & Beja, 2013; González del Pliego et al., 2016). Since most amphibians have biphasic life history, availability and quality of freshwater resources influence reproduction, larval survival and adult recruitment. Additionally, coupled interactions between terrestrial and aquatic habitats mean that agricultural practices have direct consequences on breeding habitat quality (Ficetola et al., 2011). Synergistic interactions are heightened in agriculture since land use characteristics such as chemical inputs influence waterbodies. Species-specific traits based on life history and ecology drive amphibian habitat and microhabitat use in such disturbed landscapes (Becker et al., 2010). Quantifying the benefit of microhabitats presence is crucial to designing land management strategies in production landscapes.

Our study occurs in the Western Ghats of India, an exceptionally biodiverse region, with enormous conservation challenges owing to agriculture-induced habitat loss. The Western Ghats are a global biodiversity hotspot and one of the world's oldest forested habitats. The region has >300 known species of amphibians, >80% endemism and most species were only described in the last decade and are little studied (Dinesh et al., 2019). India's amphibian research has focused on descriptions of new species and disentangling taxonomy (e.g. see Garg et al., 2017; Vijayakumar et al., 2014; Zachariah et al., 2011). Very little is known about how land management affects species diversity and turnover in these communities. A few recent studies have explored the impact of anthropogenic disturbances. They have identified morphological abnormalities in agroforests and negative consequence of hydropower dams and forest logging on amphibian species compositions (Balaji et al, 2014; Gurushankara & Krishnamurthy, 2007; Naniwadekar & Vasudevan, 2014; Seshadri, 2014). But all these studies are based on small sample size and spatial extent and do not account for imperfect detection in their survey effort. Further, the Western Ghats has faced major habitat loss and fragmentation over the last century. Much of this habitat loss can be attributed to native habitat being converted to agroforest landscapes (Ambinakudige & Choi, 2009; Das et al., 2006). Given the scale of landscape change, high rates of amphibian endemism and several species ranges that occur outside traditional protected areas, understanding ecological range distributions, habitat use and community dynamics is a critical conservation priority.

In this study, we quantify patterns of alpha and beta diversity for amphibian assemblages across areca, coffee and rubber agroforests in Karnataka's Western Ghats. These three land uses were chosen because they are the most commonly grown agroforest commodities in this landscape. We measure amphibian community response to agroforest type, and the influence of biogeography and microhabitat presence on the community and individual species. In our study, coffee agroforests are shade-grown and retain significant elements of native tree diversity which provide greater habitat heterogeneity when compared to the mix-cropped areca agroforests and the monocultured rubber agroforests (Karanth et al., 2016). Studies have also shown that coffee plantations provide secondary habitats for many forest-dependent species (Anand et al., 2008; Shahabuddin, 1997). We therefore expect species richness, beta diversity and species occurrences to be highest in coffee followed by areca and rubber agroforests. Similarly, we predicted that presence of microhabitats would significantly increase diversity across all agroforest types, with varying species-specific responses based on life history strategies.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The 1600-km-long mountain chain of the Western Ghats is a global biodiversity hotspot, with one of the highest human densities in the world (Cincotta et al., 2000; Myers et al., 2000). The region has a mixture of evergreen, moist-deciduous and dry-deciduous forests within a matrix of human-modified landscapes (Das et al., 2006). Less than 9% of the Western Ghats is within the protected area network, and much of the remaining has been modified for agriculture, mining, dams and other developmental projects (Jayadevan et al., 2020; Nayak et al., 2020).

We focused on agroforests in central Western Ghats in the state of Karnataka (Figure 1). The latitudinal gradient of the study area spans 12.5° N and 14° N, and ranges from 200 to 1930 m asl in elevation. This region has a heterogenous matrix of land uses from 30% to 50% native forest cover, 5% to 30% agroforests and 20% to 50% open agricultural fields (Kale et al., 2016). The most common agroforest commodities in Karnataka's Western Ghats are areca, coffee and rubber

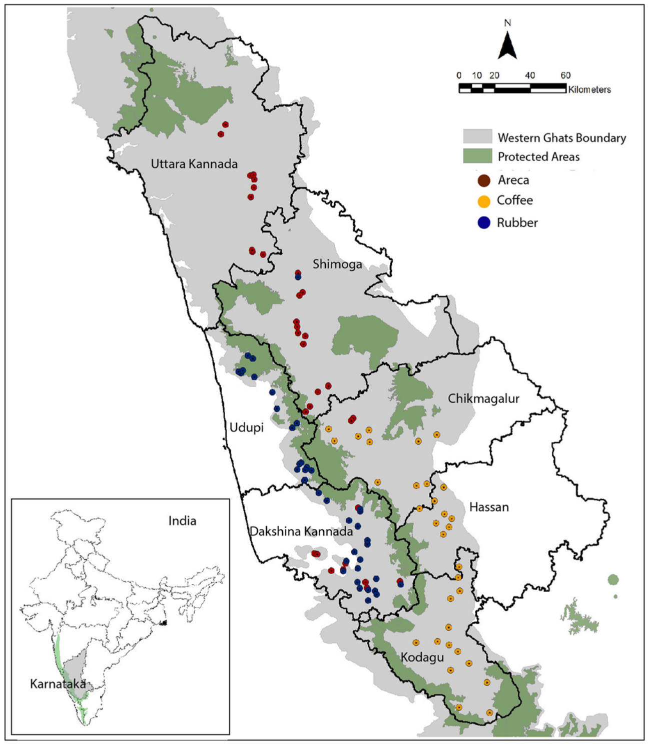


**FIGURE 1** Map of the study area with sampled locations

(Robbins et al., 2015). Within the study area, areca, a palm tree cultivated for its masticatory seed, is grown in mid to low elevations (0–800 m), and is mix-cropped with other species such as coconut, cocoa and other commercial fruiting trees. Coffee is grown at relatively high elevations (600–1300 m) and is shade-grown under a mix of native tree canopy and exotic species such as *Grevillea robusta* and *Maesopsis eminii*. Rubber is cultivated only at lower elevations (0–300 m) and is strictly maintained as a monoculture (Figure 2).

### 2.2 | Sampling methods

We surveyed 113 unique agroforests (40 areca, 33 coffee and 40 rubber). All fieldwork was conducted on privately owned agroforest land and verbal consent was acquired from all land owners before surveys were undertaken. Surveys were conducted between June and September of 2013 and 2014, in the monsoon season, when amphibians are most active. They have high calling rates in this season, allowing for both visual and auditory detection, and align the survey window with use of habitats crucial for reproduction (Duellman & Trueb, 1986). Three teams of two trained observers conducted systematic, time-constrained searches between 7:00 PM and 11:00 PM. It was assumed that the teams had equal detection probabilities and species identification capabilities. The length of the survey varied based on the size of the site from 30 to 300 min, with an average survey time of 93 min per site. The observers walked at a consistent pace, in a single direction, along foot paths, roads, cultivated areas and water bodies. We

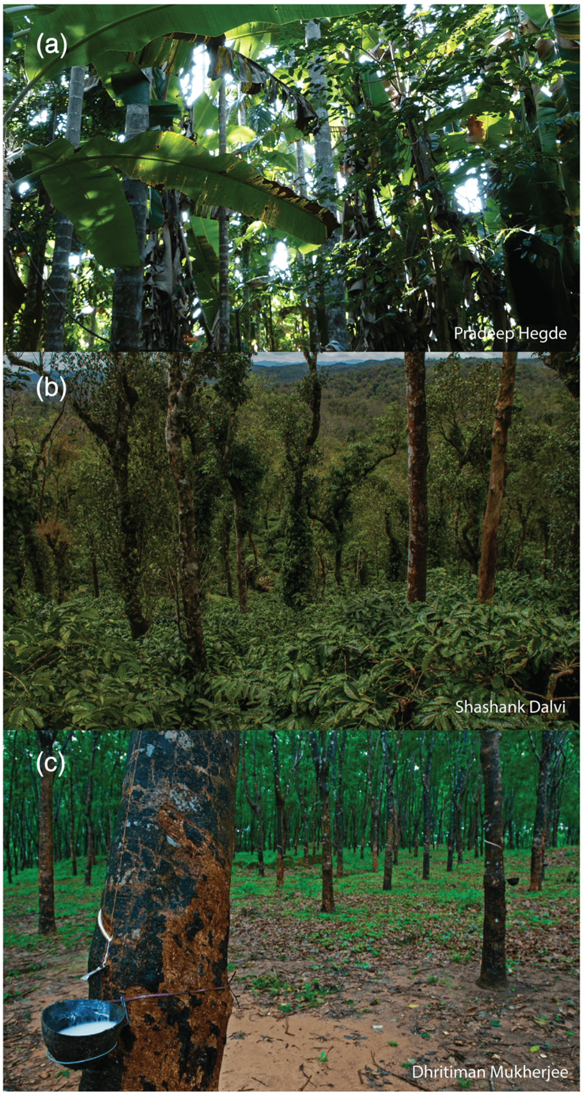


**FIGURE 2** Agroforest management showing different vegetation characteristics and canopy structure across (a) Areca, (b) Coffee and (c) Rubber

ensured that no route was retraced or resampled to prevent individuals from being recounted and to maintain independence. Observers recorded all frogs detected using visual and auditory encounter surveys (VES/AES). The two detection methods increased the probability of detecting species and individuals in the site (Ernst et al., 2006; Murrieta-Galindo et al., 2013; Ribeiro et al., 2018). Encounter of a species by either method was considered as a detection and mid to high canopy species were only observed through auditory surveys. There were no spatial constraints set on auditory detections. We attempted to identify every individual encountered to the species level based on external morphology and acoustic characteristics. Given the unsettled nature of the Indian amphibian taxonomy and the presence of multiple cryptic species meant that a subset of species remained unidentified. None of the frogs were collected, captured or handled for taxonomic identification.

## 2.3 | Analysis

We restricted the analysis to 106 of 113 surveyed sites. We removed seven sites of areca because the habitat was more akin to the dry Deccan plateau than to the Western Ghats and the species pool for this area varied drastically, making direct comparisons among agroforest types impossible. We analyzed data for the 26 species from the amphibian community that could be reliably identified in the field. Each species was assigned to one of five functional guilds – ground-dwelling, pond-dwelling, stream-dwelling, bush and tree frogs. Responses of occupancy probability to biogeography (elevation, latitude), land use (areca, coffee, rubber) and microhabitat availability (presence of ponds, streams, unpaved plantation roads) were quantified at the species level. Latitude and longitude for each site were recorded using a handheld Garmin eTrex GPS unit. Elevation was extracted from ASTER Global Digital Elevation Model with a resolution of 30 m. All biogeographic covariates were standardized before the analysis. We surveyed and recorded the presence of all available microhabitats in each site including streams, ditches, ponds, unpaved plantation roads and cultivated areas. Presence of a microhabitat was denoted as '1' and absence as '0' for each site.

## 2.4 | Multi-species occupancy model

We fit hierarchical multi-species occupancy models to the data to estimate the relationship of biogeographic characteristics, land use type and microhabitat availability on the amphibian community (Dorazio & Royle, 2005; Zipkin et al., 2010). We treated each agroforest as an independent sampling unit. At each site, the overall sampling effort (total time duration sampled) was divided into 10-min intervals, and these were treated as temporal replicates to estimate detection rates. This time interval was chosen since it allowed us to capture spatial variation in each portion of the site, cover the different available microhabitats and maximize detection of calling individuals in the study site. The data we collected during the $k$th 10-min interval for species $j$ at site $i$ is denoted by $y_{i,j,k}$, a binomial variable which takes values of 1 if the species was detected during the survey or 0 if it was not. We use $\Psi_{i,j}$, to denote the probability of occurrence where the true presence of species $j$ at site $i$ was denoted as the latent binomial variable $z_{i,j}$, where $z_{i,j} \sim$ Bernoulli ($\Psi_{i,j}$) (Dorazio & Royle, 2005; Zipkin et al., 2010).

We fit a generalized linear model to estimate the occupancy probability as a function of local and landscape variables, using a logit-link function. We fit two separate models for species occupancy ($\Psi_{i,j}$). The first model estimated the relationship of biogeography and land use variables $a$ was indicated by the parameters $\boldsymbol{\beta}_{1\text{-}4}$. Land use was coded as dummy variables with rubber being the reference against which the effect of areca and coffee was measured. The posterior for the estimated difference between coffee and areca was derived from the Markov Chain Monte Carlo (MCMC) simulations. The second model examined the relationship between microhabitat availability and amphibian occupancy. The models were fitted to the data using package R2jags (Sturtz et al., 2005) in RStudio v3.5.3 (R Development Core Team, 2019).

$$\mathrm{logit}\left(\Psi_{i,j}\right) = \beta_{0j} + \beta_{1j} \times \mathrm{Areca}_i + \beta_{2j} \times \mathrm{Coffee}_i + \beta_{3j} \times \mathrm{Elevation}_i + \beta_{4j} \times \mathrm{Latitude}_i. \quad (1)$$

$$\mathrm{logit}\left(\Psi_{i,j}\right) = \beta_{0j} + \beta_{1j} \times \mathrm{Pond}_i + \beta_{2j} \times \mathrm{Stream}_i + \beta_{3j} \times \mathrm{Road}_i. \quad (2)$$

Similarly, we included the effect of the month of survey on species-specific detection probabilities ($p_{i,j,k}$) using a logit-link function. The months of survey ranged from June to August and were coded as dummy variables with August being the reference month.

$$\mathrm{logit}\left(p_{i,j,k}\right) = v_j + \alpha_{1j} \times \mathrm{month1}_i + \alpha_{2j} \times \mathrm{month2}_i. \quad (3)$$

## 2.5 | Estimating species richness, beta diversity and dominance

We used our estimates of individual species occurrence in each site to derive metrics of alpha (species richness) and beta diversity (dissimilarity of the community between two sites) and their associated sampling error. These derived parameters of the community were calculated based on the latent variable '$z_{i,j}$' at each individual iteration of the MCMC chains. Species richness for site *i* was calculated as the sum of *z* across all species. Beta diversity was calculated using Jaccard's dissimilarity index based on the estimate of true presence for each species at each site, using the package vegan (Oksanen et al., 2013). Dominance is a measure of unevenness in species abundances within a community (Magurran, 2013). Dominance was examined using a modified Whittaker plot with *y*-axis representing mean '*z*' of each species instead of rank abundance (Whittaker, 1965). Since occupancy probability and abundance are usually positively correlated, this plot visually depicts the disproportionately high numbers of some species, relative to others in the community (Holt et al., 2002).

## 3 | RESULTS

We detected 12,012 amphibians across the 26 species and 16 genera that were included in our analyses. We detected 2694 frogs from 14 species in areca sites, 5201 frogs from 22 species in coffee sites and 4117 frogs from 13 species in rubber sites. The 26 detected species included eight species of bush frogs, four tree frogs, eight ground-dwelling frogs, four pond-dwelling frogs and two stream-dwelling frogs (Table S1). The subset of observations for which we were unable to identify individuals to taxa belonged to five different genera and were present in all three agroforest types. The distribution of unidentified observations was similar to those of known taxa with 901 unidentified detections in areca, 1520 detections in coffee and 550 detections in rubber agroforests. Unidentified detections mostly belonged to *Fejervarya*, *Indosylvirana* and *Indirana* genera.

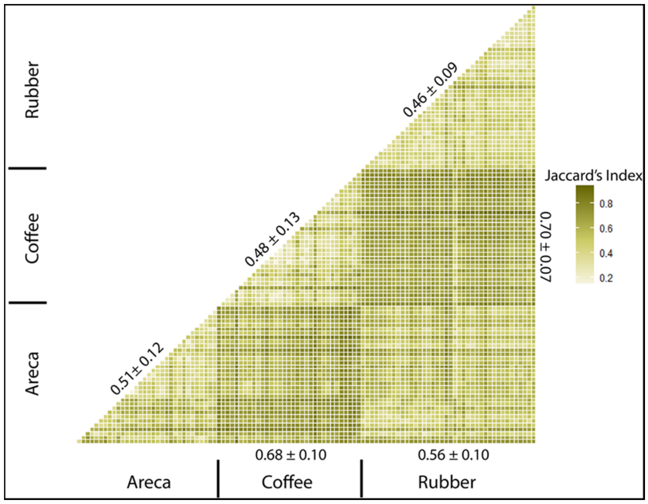


**FIGURE 3** Beta diversity comparisons within and across agroforest types

### 3.1 | Community-level responses

Estimated mean species richness per site after accounting for detection was significantly higher in coffee (11 ± 0.52 species per site) than the other two agroforest types. Species richness in rubber (7.68 ± 0.62) and areca (7.25 ± 0.58) sites was very similar.

On an average, there was less heterogeneity in species compositions within agroforest types than across them. The highest beta diversity among sites of the same agroforest type occurred among areca sites, with an average Jaccard index among pairs of 0.51 (± 0.12), followed by coffee (0.48 ± 0.13), and finally, rubber sites were the most homogenous (0.46 ± 0.09). When comparing differences in species composition between agroforest types, areca and rubber agroforests were most similar, whereas comparisons of coffee to areca and coffee to rubber had higher beta diversity (Figure 3).

Finally, we examined dominance within each of the agroforest types, as measured by the distribution of proportions of sites estimated to be occupied by each species. The shallow slope seen in rank-occupancy plots of coffee agroforests indicates lower dominance compared to areca and rubber (Figure 4). Overall, coffee supported the highest species richness and greatest beta diversity when compared to other agroforest types, and lowest dominance across the amphibian community. In contrast, areca and rubber were dominated by fewer species that were relatively ubiquitous across sites. The bush frogs *Pseudophilautus amboli* and *Raorchestes tuberohumerus* were amongst the commonest species across all sites.

### 3.2 | Species-specific responses

Response to the biogeographic variables, elevation and latitude, were species specific but not strongly associated with the functional guild of the species (Figure 5). Latitude had an unexpectedly positive association with nine species, whereas five were negatively associated and

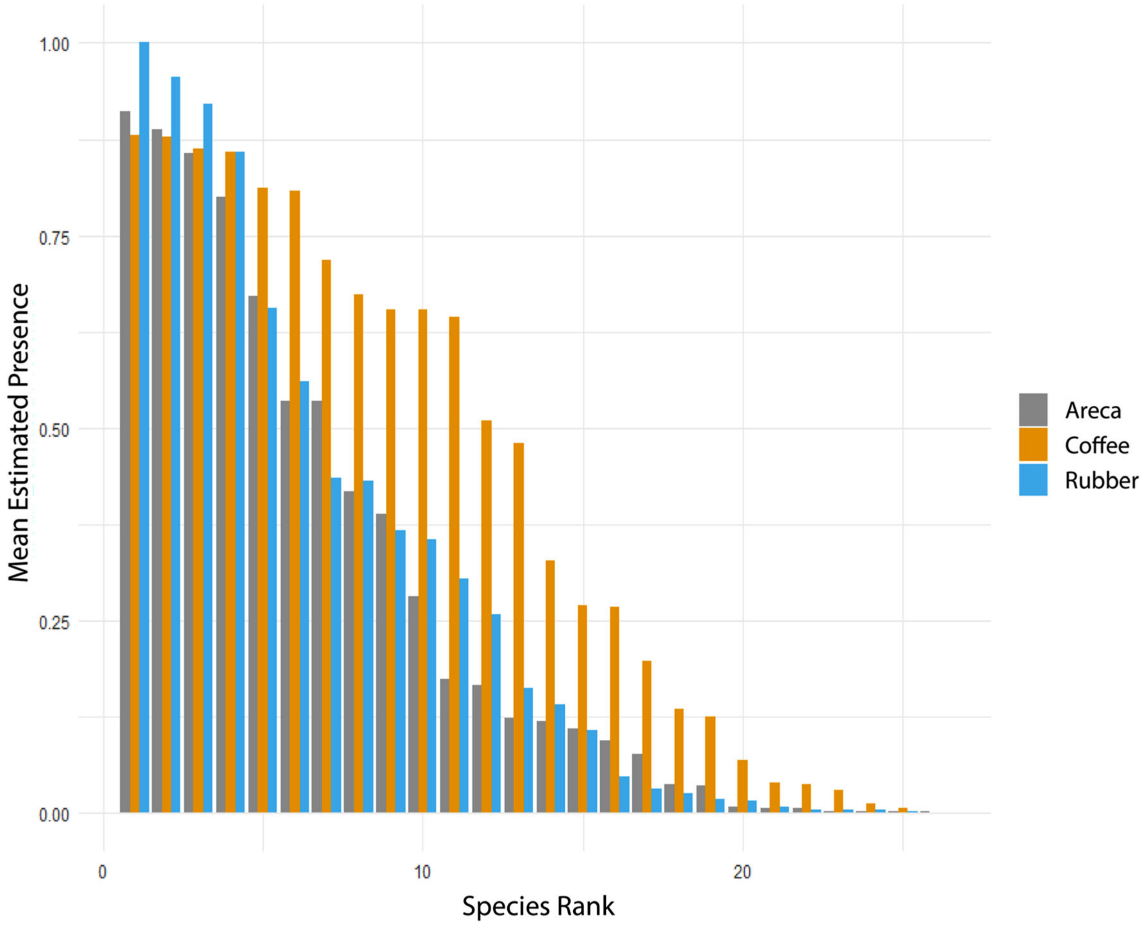


**FIGURE 4** Species dominance plot across agroforests ranked by decreasing mean estimated presence

12 species did not show any relationship with this variable (Table S1). Bush frogs showed the strongest negative association with latitude with four out of five species belonging to this guild, whereas ground-dwelling frogs showed the most positive associations with latitude. Overall, 11 species showed positive associations and six species showed negative association with elevation (Table S1). Members of the family Rhacophoridae showed the greatest positive relationship with elevation with six bush frogs and two tree frogs in this group. Amongst species that were negatively affected, four belonged to ground-dwelling, two to tree frogs and two to bush frog guilds.

For individual species, agroforest type came out as a strong predictor of occupancy for 16 species. Seven species had positive association with areca sites relative to the other agroforest types (as measured by the estimated beta coefficient), but most of them included 0 in their 95% credible interval. *Minervarya sahyadris* was the only species that showed higher occupancy probability in areca compared to coffee and rubber agroforests. Consistently across the community, species occupancy was most often positively associated with coffee, and to a lesser extent with rubber, over areca sites (Figure 6). Of species positively associated with coffee over rubber and areca, *Nyctibatrachus sanctipalustris*, *Uperodon triangularis*, *Raorchestes hassanensis* and *Rhacophorus lateralis* are the most range restricted and endemic to this region of the Western Ghats (IUCN, 2020).

The presence of microhabitats was very influential in determining overall species richness and individual species presences across agroforest types (Figure 7). Presence of ponds alone as a microhabitat was associated with an average 34.7% increase in species richness, with change in individual species occupancies varying from −2% to 327% (Table S3). The mean estimated beta coefficients showed that ponds positively affected 16 species, including five bush frogs, three tree frogs, four ground-dwelling frogs, three pond-dwelling frogs and one stream-dwelling frog (Table S2). Streams presence alone did not affect overall species richness when compared to sites with no microhabitats. Individual species responses in occupancy ranged from −59% to 273% increase with stream presence (Table S3). The mean estimated beta coefficient value across the community was weakly positive (0.03 ± 0.23) with varying individual species responses. Five species showing significant positive associations and nine more species had positive estimates with credible intervals overlapping 0, whereas only two species showed negative associations with the availability of this microhabitat. Among the five significant species, the two stream-dwelling frogs had highest estimated beta coefficients for stream presence followed by three bush frogs (Table S2).

Lastly, roads increased overall species richness by 21.5% with change in species-specific occupancy ranging from −82% to 656% (Table S3). The mean estimated beta coefficient suggests

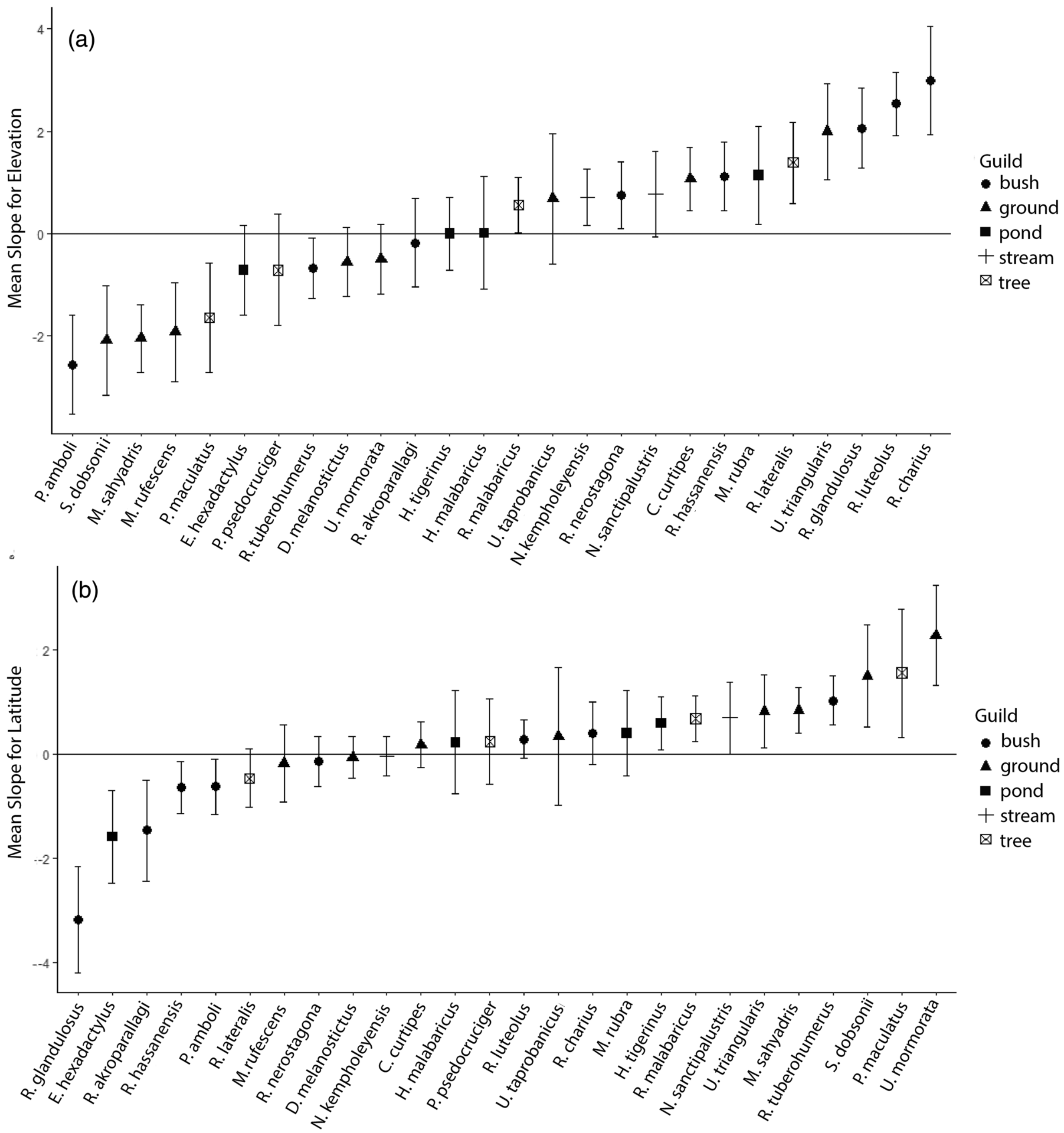


**FIGURE 5** Species-specific response to biogeographic variables: (a) mean response of species to elevation; (b) mean response of species to latitude

that road presence positively influenced occupancy for nine species and was negatively associated with two ground-dwelling species. The nine species consisted of four bush frogs, one tree frog, one pond-dwelling frog and three ground-dwelling frogs (Table S2).

Presence of all three microhabitats at a site increased predicted species richness by 75.5% with individual species occupancies expected to change by −83% to 2288%. The combination of coffee agroforest with microhabitat availability seems particularly important for four range-restricted species that have very different breeding strategies. *Nyctibatrachus sanctipalustris* is an endangered, strictly stream-breeding species for which predicted occupancy increased by 273% with stream presence. *Rhacophorus lateralis* lays foam nests on trees over stagnant pools and presence of all three microhabitats is expected to increase its occupancy by 1580%. *Uperodon triangularis* breeds in still and slow-moving water and even in tree hollows with water and presence of all three microhabitats can increase occupancy by 542%. *Raorchestes hassanensis* is a direct-developing terrestrial species. Yet, water bodies and microhabitats seem crucial, increasing their occupancy probability by 2288%. The responses for all four of these uncommon species in the study have important management consequences (Figure 7).

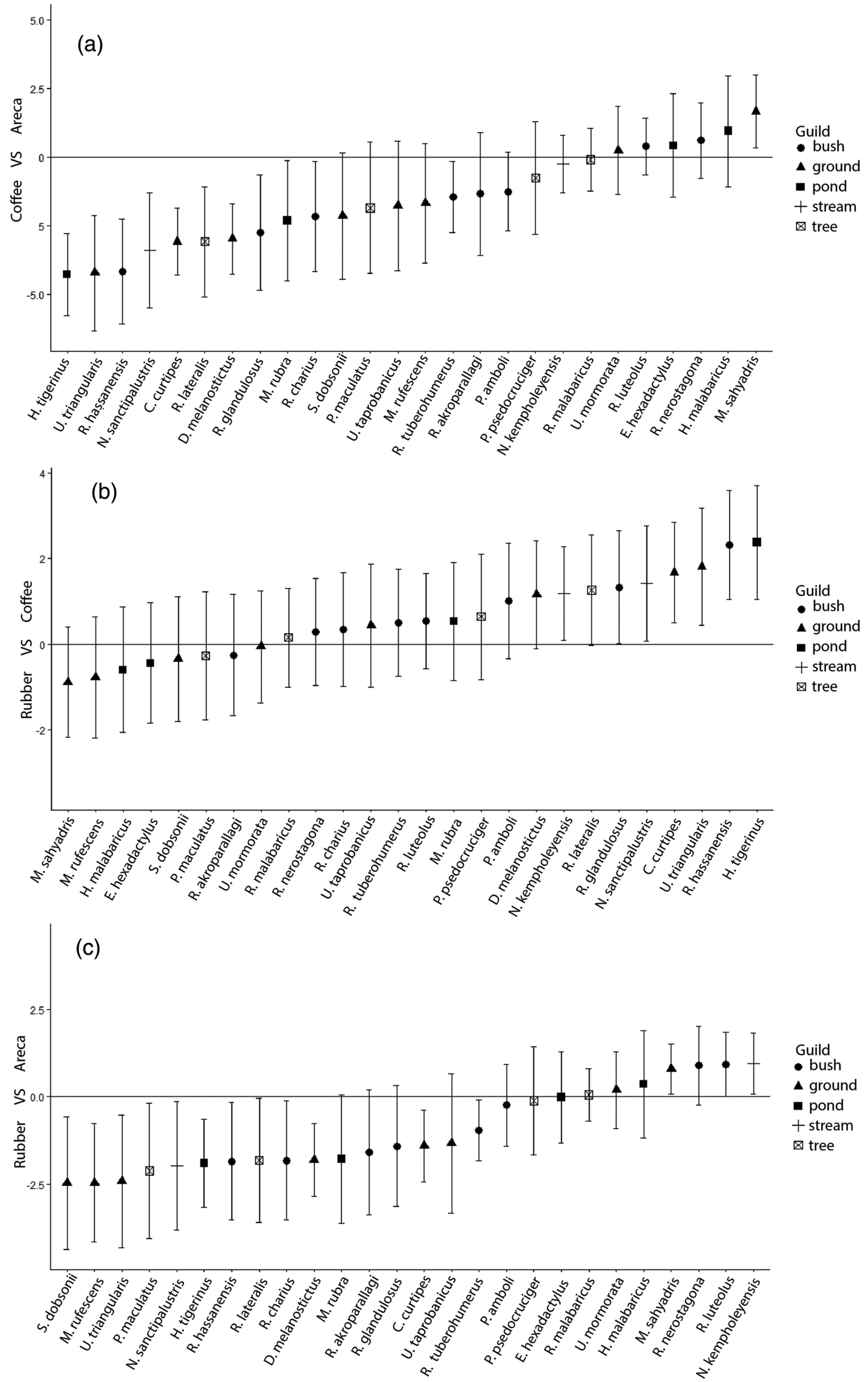


**FIGURE 6** Species-specific response to the three agroforest types: (a) effect of Areca on species occupancy compared to Coffee; (b) effect of Coffee on species occupancy compared to Rubber and (c) effect of Areca on species occupancy compared to Rubber

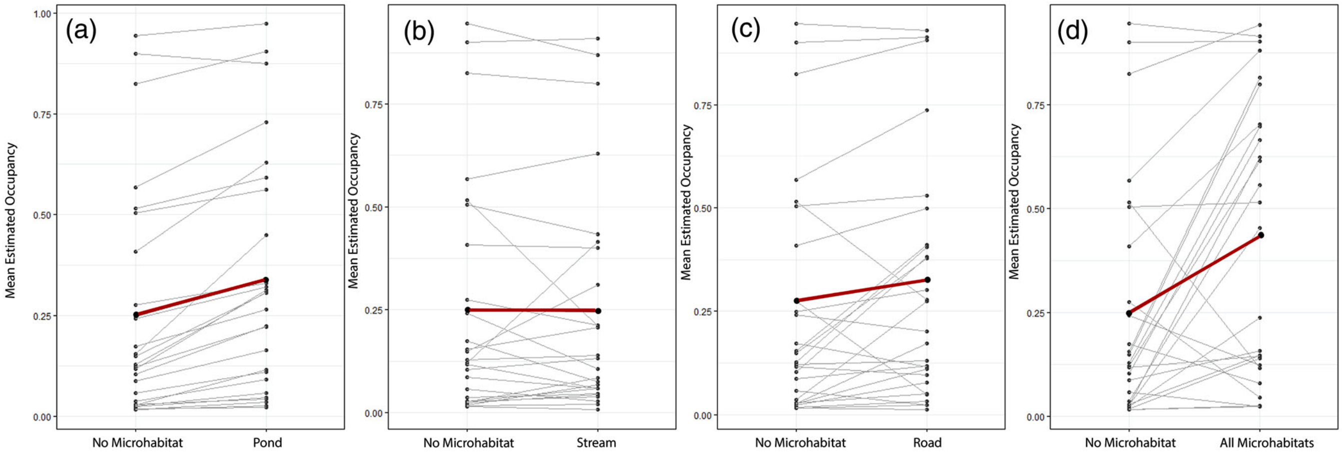


**FIGURE 7** Change in mean probability of occupancy of each species across different levels of microhabitat availability. (a) No microhabitats to only pond present. (b) No microhabitats to only stream present. (c) No microhabitats to only road present. (d) No microhabitats to all three microhabitats present

### 3.3 | Detection probabilities

The mean estimated probability of detection for each species across all sites varied from 0.03 (± 0.006) for *Kaloula taprobanica* to 0.75 (± 0.1) for *Pseudophilautus amboli*. There was significant species-specific response to the month of survey, with detection of six species showing positive association with June over August, whereas eight species showed the reverse trend. Detection of 10 species was associated strongly with July over August, whereas only five species preferred the reverse (Table S4).

## 4 | DISCUSSION

Like many biodiverse regions in the tropics, the Western Ghats face agricultural intensification and habitat loss (Kale et al., 2016). For conservation to be successful, it is becoming increasingly important to find agricultural practices that support biodiversity (Phalan et al., 2011; Tscharntke et al., 2012). Using a rigorous sampling and analytical framework, our study is among the first in the Western Ghats that has looked at community ecology of amphibians from both local and landscape scales, covering an area of almost 30,000 km$^2$. We find that agroforests in the Western Ghats provide habitats for a diverse group of amphibians. Of the three prominent agroforestry products in the region – rubber, areca and coffee – our findings highlight the importance of coffee agroforests in particular. Our results also show that the maintenance of stream and pond habitats in conjunction with plantation roads of low vehicular movement in agroforest settings is correlated to higher local-scale biodiversity. These findings provide evidence for altering land management strategies to focus on microhabitat conservation.

Agricultural practices that maintain diverse and heterogeneous vegetation structure improve the conservation value of these landscapes (De Beenhouwer et al., 2013; Wanger et al., 2010). Our findings, along with those of Karanth et al. (2016), demonstrate that shade-grown coffee agroforests have better land management strategies for sustained biodiversity conservation. Between areca and rubber agroforests, we predicted the former to show greater species richness because of its multi-cropped system with greater tree diversity compared to the monoculture practiced in rubber farms. Areca and rubber agroforests revealed comparable species richness, values and similar results were documented for bird diversity across the same study sites (Karanth et al., 2016). In Thailand, another recent study found butterflies, birds and reptiles had similar diversity indices between rubber monocultures and other agroforests (Warren-Thomas et al., 2020). In our study system, one possible explanation for these findings is that rubber farms were generally closer to primary forests than areca and proximity to primary forests might be making species richness higher. Another study also showed increase in bird species richness in rubber agroforests with higher surrounding forest cover (Sreekar et al., 2016).

In addition to influencing species richness, habitat degradation in agriculture–forest matrix can influence community composition and evenness (Russildi et al., 2016). Increased disturbance can cause decline in beta diversity and homogenization of communities (Nowakowski et al., 2018). Our findings suggest community composition was consistent within each agroforest type with Areca sites being slightly more dissimilar than others, but this may be because mean distance and elevation range between areca sites were greater than for the other two agroforests. Among the three agroforest types, coffee was the most dissimilar to the other forest types. The lower indices between areca and rubber demonstrate that both communities were more homogenized with strong dominance structure represented by two species of bush frogs: *Pseudophilautus amboli* and *Raorchestes tuberohumerus*. These are probably generalist species and are able to adapt to drastically modified habitats in the lower elevations of the Western Ghats. The assemblage in coffee, however, is both diverse and contains a more even species composition. Ant assemblage across coffee and forests have shown similar patterns, where mass effects from shade trees reduce dominance structure and increase the probability of rare species occurrence (Livingston et al., 2013).

Given the geographic scale of this study, we also accounted for the influence of biogeographic variables on amphibian occupancies. Life-history traits are known to strongly influence the nature of species responses to biogeographic variables (Pillsbury & Miller, 2008). Environmental tolerance limits have allowed species to evolve and occupy varying latitudinal ranges from tropics to poles, with overall species richness being negatively associated with latitude (Sommer et al., 2014). The lack of a negative trend in our study maybe because of the narrow latitudinal gradient in the study area and the confounding effects of spatial distribution in the agroforest types. Since coffee is grown only in the mid latitudes and at high elevations of our study area, it could have biased the results of the other variables.

Elevation is another important biogeographic variable that often produces mid-domain effect in species richness (Brehm & Kluge, 2007; McCain, 2004). In montane regions, individual species distributions are highly governed by elevation-driven niche availability, consequently creating local endemism and turnover (Poynton et al., 2007). The positive effect of elevation on 12 species in our study has significant conservation consequences in the light of climate change. As global temperatures rise, species distributions are expected to move latitudinally towards the poles and altitudinally to cooler mountain tops (Chen et al., 2011). High-elevation montane species will have reduced opportunity to shift their distributions along elevational or latitudinal axes to new climatic niches. Our study provides baseline range information, from which future research can examine range shifts caused by climate change. Climate change can also cause indirect effects on amphibians by affecting crops and cropping patterns of these agroforests. Nearly 50% of global area suitable for coffee production is predicted to be lost to climate change creating volatile prices in the market (Bunn et al., 2015). This is likely to cause land use conversion from coffee to less biodiversity-friendly farming practices with negative consequences for the ecology of the Western Ghats (Robbins et al., 2015).

At the local scale, presence of specific microhabitats and breeding sites can strongly influence amphibian presence and abundance (da Silva et al., 2011; Ficetola & De Bernardi, 2004; Thorpe et al., 2018; Wassens et al., 2010). Our results also suggest that inclusion of ponds in agroforests can greatly enhance species richness of all species in the community and not just pond-breeding amphibians. Managing networks of ponds across cultivated regions of the Western Ghats can provide 'pondscapes' that hugely enhance the biodiversity potential of agroforests (Hill et al., 2018). Further studies could examine the efficacy of constructing ponds in these landscapes to provide better breeding habitats, as this has known to positively affect threatened amphibian populations in many scenarios (Brand & Snodgrass, 2010; Romano et al., 2014; Magnus & Rannap, 2019). On the contrary, ponds in agricultural systems are known to contain higher concentrations of agrochemicals that negatively influence amphibians. Studies show that the presence of herbicides like atrazine in water affects amphibian reproduction by demasculinizing and feminizing adult males (Hayes et al., 2010). The agroforest managers in our study area also use glyphosphate-based herbicides, soil fertilizers, copper-based fungicides and chemical pesticides. A study in coffee plantations of Western Ghats shows increased levels of morphological abnormalities and dysregulation of biomarkers in the liver and brain of frogs (Hegde et al., 2019). Therefore, while ponds provide essential microhabitat, the water quality in these agroforests needs to be studied further.

Stream presence positively influenced occupancy of five species with *Nyctibatrachus* genus showing greater benefits across the assemblage. Despite being direct developing species, some bush frogs also preferentially used vegetation near water bodies indicating the importance of these microhabitats (Hertwig et al., 2012). It is possible that ponds and streams provide ecosystem services like microclimate and soil moisture regulation within agroforests (Rolando et al., 2017).

Surprisingly, our final microhabitat predictor, roads, also demonstrated a positive relationship with amphibian occupancy in our study. Roads are not usually considered a microhabitat for amphibians. They restrict movement, increase mortality and modify population dynamics (Gibbs & Shriver, 2005; Eigenbrod et al., 2009; Garcia-Gonzalez et al., 2012). The only evidence of increased road use by amphibians is restricted to studies of roads that have storm-water drainage systems that act as additional breeding habitats (O'Brien, 2015). Unpaved plantation roads in our study area have low vehicular movement, which likely reduces risk of mortality (Sutherland et al., 2010). These roads also become covered by grass and herbaceous vegetation in the monsoon and have depressions filled with rainwater which could potentially provide temporary breeding habitats.

Our study highlights the importance of identifying local and landscape features in agroforests which can be managed to maximize amphibian diversity. We found greater diversity in our most complex cropping system, suggesting that incorporating native tree elements, like the shade trees in coffee agroforests, could improve amphibian diversity in areca and rubber landscape. Land management strategies need to incorporate a multipronged approach to habitat and species conservation. Microhabitats are of particular importance, and conserving more than one microhabitat can significantly increase biodiversity potential of agroforests. Preserving freshwater bodies like ponds and streams and maintaining natural stream flows are crucial for provisioning of breeding habitats for amphibians (González del Pliego et al., 2016). Incorporating these land management practices, particularly in rubber agroforests, is critical since it had much fewer native trees and breeding microhabitats than coffee and areca.

The benefits of remnant forests and environmentally friendly agroforestry practices extend beyond biodiversity (Valdés et al., 2020). Land management approaches such as a switch from chemical to organic farming and shade-tree maintenance provide a spate of ecosystem services like pest control, pollination, nutrient safety net and soil fertility provisioning that help directly improve crop yields in agroforests (Mitchell et al., 2014; Kuyah et al., 2017). While agricultural intensification may be inevitable in some parts of the world, there is a growing need to provide spaces for wildlife within and not just separate from human-modified landscapes (Phalan et al., 2011; Tscharntke et al., 2012). Projected climate change, volatile market prices and other socio-political dynamics in the region make conservation objectives challenging (Robbins et al., 2015). High labour costs and unavailability of labour have also been among the biggest challenges for land owners and have resulted in increased chemical inputs, land use conversions and land abandonment (Robbins et al., 2021; Sreeja et al., 2021). Emphasizing ecosystem services along with conservation benefits can allow conservationists to frame the support for nature in utilitarian terms, allow land owners to market their commodities as biodiversity friendly and make it a mainstay of policy agenda for both human and environmental well-being (Gómez-Baggethun et al., 2010). This study provides evidence-based solutions for land management in tropical, biodiverse, agroforest systems. Future research in the field of agrobiodiversity needs to focus on using interdisciplinary approaches and combine ecological and social needs to better manage these production landscapes.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHORS' CONTRIBUTIONS

V.S., S.D. and K.K.K. conceived the study and designed the methodology. V.S. and S.D. collected the data. V.S. and D.M. designed the analytical framework and analyzed the data. V.S. and D.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

The data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.c2fqz6192 (Sankararaman et al., 2021).

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